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Shifting interaction strength between estuarine mysid species across a temperature gradient

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Abstract

In many coastal regions, mean coastal atmospheric and water temperatures are projected to shift as climate change ensues. Interaction strengths between organisms are likely to change along with environmental changes, given interspecific heterogeneity in responses to physico-chemical variables. Biological interaction outcomes have the potential to alter food web production and trophic level biomass distribution. This is particularly pertinent for key species that are either abundant or play disproportionately large roles in ecosystem processes. Using a functional response approach, we quantified the effects of shifting temperatures on interactions between key mysid species- sympatric in their distribution across a biogeographic transition zone along the east coast of South Africa. The *Rhopalophthalmus terranatalis* functional response type toward *Mesopodopsis wooldridgei* prey was independent of temperature, with all treatments producing Type II functional responses. Temperature effects on predator-prey dynamics were, however, evident as interaction strength was greatest at 21^{o}C, as measured by maximum feeding rates. Unlike maximum feeding rate, attack rates increased linearly with increasing temperature across the experimental treatments. Our findings suggest that interaction strength between the mysid shrimp species is likely to vary spatially along the current length of their sympatric distribution and temporally in certain regions where temperatures are projected to change. Such experimental interaction investigations are becoming increasingly important given our relatively poor understanding of the consequences of environmental change for effects on interactions among species and their wider ecosystem implications.

Keywords: Biogeographic zones; climate change; functional response; predator-prey; *Mesopodopsis wooldridgei*; *Rhopalophthalmus terranatalis*.

Introduction

The greatest uncertainty when predicting consequences of environmental change on ecosystems is determining their effects on interactions among species (Daufresne et al., 2009; Gilbert et al., 2014). Mean coastal atmospheric and water temperatures are predicted to be affected as climate change ensues (Mead et al., 2103). Given inter-specific differences in thermal optima, tolerance and performance, temperature changes can have implications for predator-prey interactions between species (Englund et al., 2011). Variable interaction outcomes have the potential to further alter food web production and biomass distribution across different trophic levels in marine ecosystems (O'Connor et al., 2009; Le Quesne and Pinnegar, 2011). Compiling experimental datasets across a range of taxa is, therefore, important for understanding and predicting biotic responses to varying environmental conditions (Gilbert et al., 2014; South et al., 2018). This is particularly pertinent for key species that are either abundant or play a disproportionately important role in trophic dynamics.

The South African coastline transitions from a sub-tropical to a cool-temperate climatic zone (Wooldridge and Deyzel, 2012). Many species of the region are widespread, spanning a broad range of nearshore habitats characterized by different thermal conditions (Montoya-Maya and Strydom, 2009; Wooldridge and Deyzel, 2012). *Rhopalophthalmus terranatalis* and *Mesopodopsis wooldridgei* are mesozooplanktonic mysid species that are abundant in estuaries along the temperate coastline of South Africa (Montoya-Maya and Strydom, 2009; Wooldridge and Deyzel, 2012) and are considered integral to estuarine food webs in the region (Wooldridge, 1986). The species are, however, sympatric from the cool-temperate south and west coasts (Montoya-Maya and Strydom, 2009) to the warm-temperate/sub-tropical biogeographic

transition zone along the east coast of South Africa (Wooldridge and Deyzel, 2012). *Rhopalophthalmus terranatalis* distribution, however, reportedly extends further up the coastline well into warmer waters of the subtropical region (Ortega-Cisneros and Scharler, 2015). Since *M. wooldridgei* comprises an important component of the diet of *R. terranatalis* (Wooldridge and Webb, 1998), we wanted to assess how temperature mediates predator-prey interaction outcomes between these mysid species.

As a measure predatory interaction strength, a functional response (FR) approach was employed. The FR of a predator is the relationship between prey density and consumption (Holling, 1959) and is routinely used by ecologists to gain insight into predation dynamics (Holling, 1959; Rall et al., 2012; Wasserman et al., 2016; Dick et al., 2017 and references therein). Three forms of the FR are typically considered (Hassell, 1978; Alexander et al., 2013). Type I FRs are usually associated with filter feeders whereby there is a density independent response characterized by the presence of an abrupt plateau in consumption as a result of handling constraints (Hassell, 1978; Jeschke et al., 2004; Alexander et al., 2013). Type II FRs are, however, inversely density-dependent with prey consumed in high proportion at low densities while at high densities consumption occurs at a decelerated rate until an asymptote is reached (Alexander et al., 2013). The Type III FR is a density dependent sigmoidal response with low prey consumption at low prey densities (Hassell, 1978; Alexander et al., 2013). Each FR Type is, therefore, thought to have different implications for prey population stability with Type II FR's considered more de-stabilizing for prey populations than the Type III FRs (Hassell, 1978).

Ricciardi et al. (2013) posit that individual performance will decline as differences between ambient conditions and physiological optimum increase (environmental matching hypothesis). This is pertinent in predator-prey systems given that the performances of both are integral in interaction outcomes, and the level of environmental matching may differ between predator and prey. Predator functional responses are, therefore, sensitive to changes in environmental conditions. Temperature, for example, has been shown to have implications for functional response type and magnitude, with implications for prey population dynamics (e.g. Cuthbert et al., 2018; South et al., 2018). As such, in the present study we specifically wanted to test whether (1) the predator functional response type of *R. terranatalis* toward *Mesopodopsis wooldridgei* is dependent on temperature, and (2) varying temperature alters the strength of the functional response. Such information would be useful for understanding how *R. terranatalis-M. wooldridgei* predator-prey dynamics vary spatially, along the length of their current sympatric distribution. It would also add insight into how interaction strength may vary per region as climate change ensues, since localized ocean temperatures are projected to increase or decrease, depending on the region and oceanographic features (Mead et al. 2013).

Methods

Mysids were collected from the middle reach of the permanently open Kariega Estuary (33.630640°S; 26.639894°E) in the Eastern Cape, South Africa. At the time of collection the salinity and temperature recorded was 35ppt and 19 °C, respectively. Animals were collected from a boat by towing a zooplankton net (57 cm diameter, 200 µm mesh) horizontally along the axial length of the estuary, at ~10 cm beneath the water surface. Zooplankton was preliminarily sorted on the boat through a series of size fractionated filtration whereby all larger components

of the zooplankton (including the large predatory *R. terranatalis*) were separated from intermediary-sized organisms (*M. wooldridgei*), while all small organisms were discarded on site.

In the laboratory, *R. terranatalis* and *M. wooldridgei* were separated into aerated glass aquaria (46 × 23 × 60 cm) in temperature controlled environmental rooms at a 12:12h (light:dark) photoperiod cycle. Aquaria contained estuarine water from the collection site filtered through 0.7 µm mesh sieve. All mysids were kept at a salinity and temperature of 35 ppt and 19 °C, respectively, for 24 h after collection prior to acclimation regimes. Animals were then acclimated to one of four treatment temperatures; 13 ± 0.5 °C, 17 ± 0.5 °C, 21 ± 0.5 °C or 25 ± 0.5 °C, for 5 days during which time they were fed daily on crushed commercial fish flakes (TetraMin® tropical flakes).

Individual *R. terranatalis* (total length ± SD; 14 ± 0.5 mm) were each presented with *M. wooldridgei* (7 ± 0.5 mm) at 1 of 8 prey densities (2, 4, 6, 8, 10, 20, 30 or 40 individuals, $n = 4$ per prey density) for each temperature treatment. Experiments were carried out in circular polyethylene containers (60 mm deep, 110 mm diameter) filled with 500 mL aerated, filtered estuarine water (35 ppt salinity) from the collection site. The experimental containers were placed in temperature regulated water baths set to the same temperature as the environmental rooms. *Mesopodopsis wooldridgei* prey were stocked into containers 2 h prior to the introduction of the predator. Upon predator transferral, containers were covered with 500µm nylon mesh to prevent mysid escape, and left undisturbed for 12 h under dark conditions. Controls were also run at the same temperatures and prey densities ($n = 4$) for the same length of time, but with no

136 predators. At the end of each trial, samples were collected in a 60 μm mesh sieve and the prey
137 counted.
138
139 Overall prey consumption was analysed with respect to 'temperature' and 'prey supply'
140 and their interactions using generalised linear models (GLMs) assuming Poisson error
141 distribution as residuals were not overdispersed in relation to degrees of freedom. Non-
142 significant terms and interactions were removed stepwise to satisfy the minimum adequate model
143 (Crawley, 2007), with χ^2 used to compare residual deviance between models and report the
144 relevance of factors to the dependent variable. We employed the 'multcomp' package in R
145 (Hothorn et al., 2008) to undertake post-hoc comparisons of significant effects in the resulting
146 model using Tukey's comparisons. Functional responses (FRs) were analysed using the 'frair'
147 package in R (Pritchard et al., 2017). Logistic regression was used to infer FR types, whereby a
148 significantly negative first order term is indicative of a Type II FR (Juliano, 2001). As prey were
149 not replaced as they were consumed, we fit Rogers' random predator equation (Juliano, 2001) to
150 account for prey depletion:
151
152 $$N_e = N_0(1 - \exp(a(N_e h - T)))$$ Eqn. 1.
153
154 where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h
155 is the handling time and T is the total experimental period. We applied the Lambert W function
156 in R due to the implicit nature of the random predator equation (Bolker, 2008). Functional
157 responses were non-parametrically bootstrapped (n = 2000) to construct 95% confidence
158 intervals (CIs) around FR curves. This procedure enables data to be considered at the population-

level as opposed to the sample-level, with a lack of overlap in CIs sufficient to ascribe differences between FRs (see Barrios-O'Neill et al., 2014). All statistical analyses were undertaken in R v3.4.2 (R Core Team, 2017).

Results and Discussion

Survival in control treatments exceeded 98.5% at all temperatures, and so experimental deaths were attributed to predation by mysids, which was also directly observed. Overall consumption was significantly affected by temperature ($\chi^2 = 10.590$, d$f = 3$, $p = 0.014$), an effect driven by significantly greater predation at 21 °C than at 13°C ($z = 2.607$, $p = 0.045$). Overall consumption increased under greater prey density ($\chi^2 = 79.948$, d$f = 7$, $p < 0.001$) and there was no significant 'temperature × prey density' interaction effect ($\chi^2 = 8.46$, d$f = 21$, $p = 0.993$). Type II FRs were detected irrespective of temperature (Table 1). Overall, *R. terranatalis* exhibited the highest magnitude FR at 21 °C (Fig. 1). Attack rates increased concurrently with temperature (Table 1), and were significantly greater at 25 °C compared to 13 °C and 17 °C as CIs did not overlap at low-intermediate prey densities. Functional responses were indifferent between 13 °C and 17 °C as CIs overlapped at all prey supplies here. Functional response CIs at 21 °C did not overlap with those at 13 °C, and diverged from CIs at 17 °C at intermediate-high densities, indicating significantly lower handling times at 21 °C and, inversely, greater maximum feeding rates at this temperature regime.

The *R. terranatalis* functional response type toward *M. wooldridgei* prey was independent of temperature, with all treatments producing Type II FRs. However, temperature effects on predator-prey dynamics were clear. The results reflect the findings of Rall et al.

(2012), who showed that while attack rate may increase linearly with temperature, handling time and temperature relationships are often non-linear. In the present study, interaction strengths were greatest at 21 °C as maximum feeding rates were high at this temperature, while those of 13 °C, 17 °C and 25 °C temperature treatments were similar. Unlike the maximum feeding rates, attack rates increased linearly with increasing temperature and these findings have implications for *R. terranatalis – M. wooldridgei* interactions since the species span different biogeographic zones in sympatry (Montoya-Maya and Strydom, 2009; Wooldridge and Deyzel, 2012). Furthermore, along the South African coastline temperatures are projected to increase in certain regions and decrease in others, due to increased upwelling events (Mead et al., 2013). The results of the present study, therefore, suggest that interaction strength between the mysid shrimp species is likely to vary spatially along the current length of their sympatric distribution and temporally in certain regions where temperatures are projected to change.

Wooldridge and Webb (1998) calculated that *R. terranatalis* predation could result in local removal of *M. wooldridgei* based on predator feeding rates (at one temperature) and estuary predator and prey numbers. The persistence of a Type II FRs across temperature treatments further highlights the potential significance of *R. terranatalis* predation towards *M. wooldridgei* in estuarine ecosystems where they commonly co-occur and interact. Unlike Type III FRs, Type II FRs are associated with prey extinction likelihood as they have a de-stabilizing effect on prey populations since proportional consumption is high even at low prey densities (Taylor and Collie, 2003; Ward et al., 2008). While overall consumption was highest at an intermediate temperature, attack rates were greatest at the highest temperature, decreasing linearly with a reduction in temperature. This suggests that at low densities *M. wooldridgei* are at increased risk

of predation from *R. terranatalis* under high temperature conditions relative to cooler temperatures. The results of Wooldridge and Webb (1998) and this study suggest that small populations of *M. wooldridgei* at the edge of their thermal limits may be more susceptible to biotic-driven localised extinctions.

The experimental temperature range employed spanned the temperature extremes found in estuaries in which the mysid species co-occur (Montoya-Maya and Strydom, 2009; Wooldridge and Deyzel, 2012). The effects of temperature on the mysid species interactions are evident, but the mechanisms facilitating these observations need further elucidation. The relationship between temperature and predator-prey interaction strength is inherently complex as predation differs from conventional measures of performance in that it is dependent on both the predator and the prey (Rall et al., 2012, Ohlund et al., 2014). Both interacting species are affected by environmental conditions such as temperature variability (Ziarek et al., 2011; Rall et al., 2012) and levels of environmental matching may differ between predator and prey. Environmental matching considerations are important when assessing predation effects (Ricciardi et al., 2013). Future work should, therefore, include measures of predator and prey thermal optima, and performance such as swimming, attack and escape speeds across a range of relevant temperatures. Such an approach would add insight into how inter-specific variations in performance facilitate interaction outcomes and could explain how maximum feeding rates were similar at the lower and upper end of the experimental temperature ranges. Such pairwise interaction investigations are a fundamental component of food web ecology and are central to the mechanistic understanding of predator-prey dynamics (Rall et al., 2012; Barrios-O'Neill et

al., 2014; Dick et al., 2017). Key trophic species are particularly important in this regard given that their interaction outcomes likely have increased community-wide implications.

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Table 1. First order terms resulting from logistic regression of proportion of prey consumed as a function of prey supply and parameter estimates derived from Rogers' random predator equation. a = attack rate, h = handling time, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

Temperature (°C)	**1st order term**	***a***	***h***
13	-0.02549*	0.21864**	0.17711*
17	-0.03044**	0.27237**	0.22125**
21	-0.03540***	0.46539***	0.15053***
25	-0.04927***	0.70050**	0.24230***

Fig. 1. Functional responses of *Rhopalophthalmus terranatalis* (Mysidae) predators towards common focal *Mesopodopsis wooldridgei* prey at a) 13 °C, b) 17 °C, c) 21 °C and d) 25 °C. Shaded areas are bootstrapped (n = 2000) 95% confidence intervals. Raw data points are overlaid.